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A Comparison of Some Electrical and Anatomical Characteristics of the Electric Eel, *Electrophorus electricus* (Linnaeus).

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(Text-figures 1-7).

In a previous paper[2] it has been shown that the major and minor electrical discharges of the electric eel, *Electrophorus electricus* (Linnaeus), are produced respectively by the large organs and the organs of Sachs. It has also been shown[3] that the current produced in a conductor joining two points along an electric organ could be approximately accounted for by ascribing to the segment of the organ between the two points a constant electromotive force and a variable internal resistance and considering it shunted by a constant leakage resistance which may be attributed to the adjacent tissue. Except during the discharge the internal resistance of the segment is assumed to be so much higher than the leakage resistance that the potential difference is negligible between different points along the organ. The discharge is attributed to a transient drop in the internal resistance, allowing the electromotive force to produce a current.

Let R denote the internal resistance of a segment of the organ at the peak of the discharge, when the resistance is at its minimum. Let E denote the electromotive force of the segment and let r denote the leakage resistance, of the adjacent tissue. Let R′ denote the resistance of a conductor connected between electrodes in contact with the fish at the ends of the segment and let V denote the potential difference between these electrodes at the peak of the discharge. Then these quantities may be shown to be related by an equation, which may for the present purpose conveniently be written in the form

$$\frac{E}{V}=\frac{R}{R'}+\frac{r+R}{r} \quad . \tag{1}$$

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[2] Coates, C. W., R. T. Cox, & L. P. Granath. The Electric Discharge of the Electric Eel, *Electrophorus electricus* (Linnaeus). *Zoologica,* Vol. XXII (Part 1), No. 1, April 5, 1937.

[3] Cox, R. T., & C. W. Coates. Electrical Characteristics of the Electric Tissue of the Electric Eel, *Electrophorus electricus* (Linnaeus). *Zoologica,* Vol. XXIII (Part 2), No. 8, July 14, 1938.

If R′ is varied in this equation, V varies with it in such a way that for every change in 1/R′ there is a proportional change in 1/V. Consequently the graph of 1/V plotted against 1/R′ will be a straight line. In Text-fig. 1 are plotted measurements of peak voltages obtained with various external resistances joined to electrodes 10 cm. apart on the large organ of an electric eel 103 cm. long. The sets of points indicated by different signs show sets of observations made at several different times. It will be seen that the points fall near to a straight line. (It should perhaps be pointed out that this does not prove the hypothesis of a variable internal resistance and constant electromotive force. This must be based upon other evidence discussed in the previous paper. The equation just given would still be valid if the internal resistance were constant and the electromotive force variable).

From the equation (1), when 1/R′ is zero, then

$$V = \frac{E\,r}{r + R} \;. \tag{2}$$

This corresponds to the case in which there is no external conductor between the electrodes. If the leakage resistance r is much greater than the internal resistance R, the observed peak voltage V will be nearly equal to the electromotive force E.

If, in the equation (1),1/V is set equal to zero, then

$$\frac{1}{R'} = -\left(\frac{1}{r} + \frac{1}{R}\right) . \tag{3}$$

Since negative values of the resistances are impossible, this case corresponds to no actual observation. But the line determined by the actual observations may nevertheless be extended, as in Text-fig. 1, to meet the axis of 1/R′ and the intercept may be noted to determine 1/r + 1/R. If the leakage resistance r is otherwise known, this last result makes it possible to determine R, the internal resistance of the segment of the electric organ. With both these resistances known, the intercept on the axis of 1/R′ may be used to determine the electromotive force E.

With the electric eel already mentioned the leakage resistance r was measured between electrodes 10 cm. apart along the portion of the body containing the electric organs. The measurement was made by observing the current passing through the body of the eel between the electrodes when a measured potential difference was applied to them. The peak voltages produced between the same electrodes in the same positions on the fish with various resistances connecting them were measured in both the major and minor discharge by means of a cathode-ray oscillograph. The electromotive force and the internal resistance of each segment 10 cm. long down the length of the organs were determined as already explained and as illustrated by Text-fig. 1.

The results of these observations and computations are shown in Table I for the major discharge and Table II for the minor discharge. The distances recorded in the first column of each table are measured from the anterior end of the anal fin, which is a convenient point of reference almost at the anterior end of the large organ.

TABLE I.

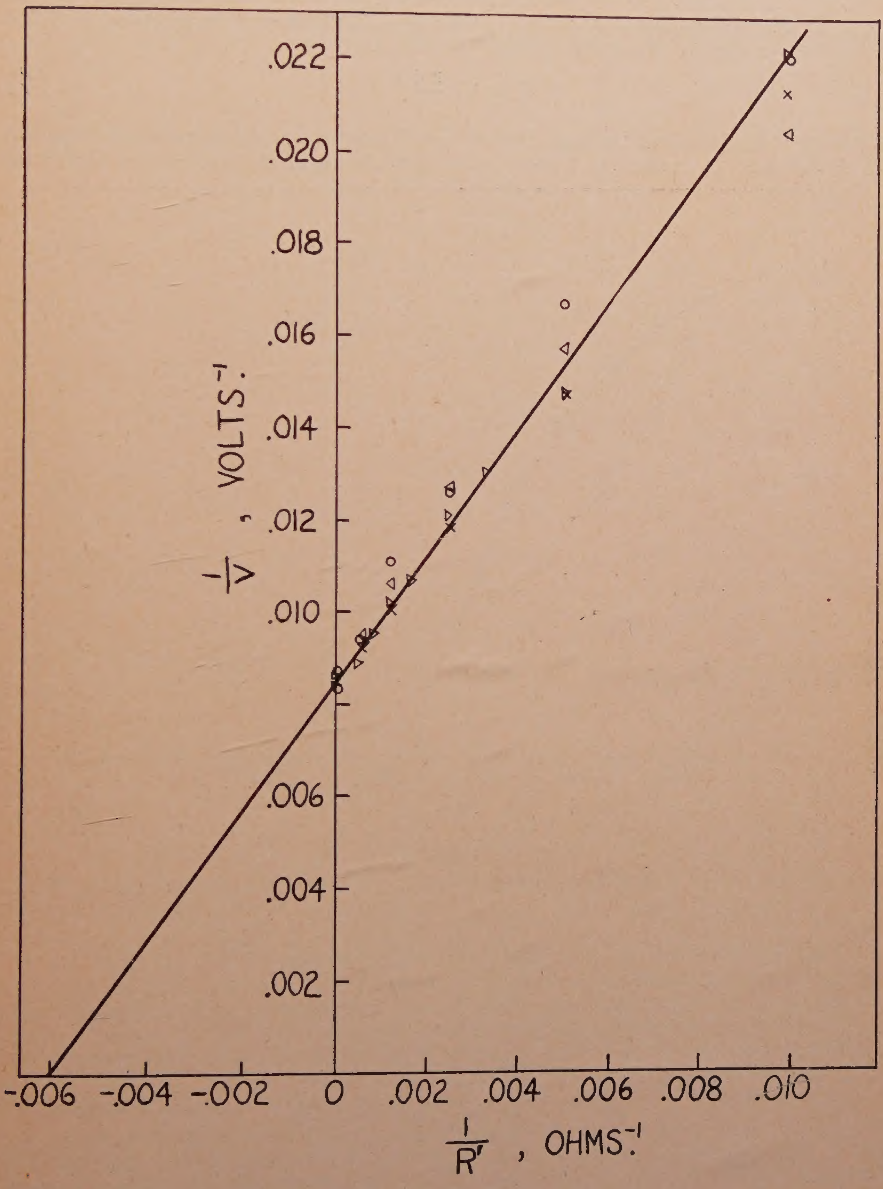
Major Discharge.

Positions of Electrodes, cm.	r, ohms	R, ohms	E, volts
0, 10	750	175	160
10, 20	765	210	150
20, 30	725	210	130
30, 40	675	180	90
40, 50	600	215	60
50, 60	550	325	30
60, 70	625	605	22
& 60, 80	1215	850	32

TABLE II.

Minor Discharge.

Positions of Electrodes, cm.	r, ohms	R, ohms	E, volts
30, 40	675	475	4.8
40, 50	600	365	7.7
50, 60	550	365	12
60, 70	625	475	20
70, 80	925	780	22



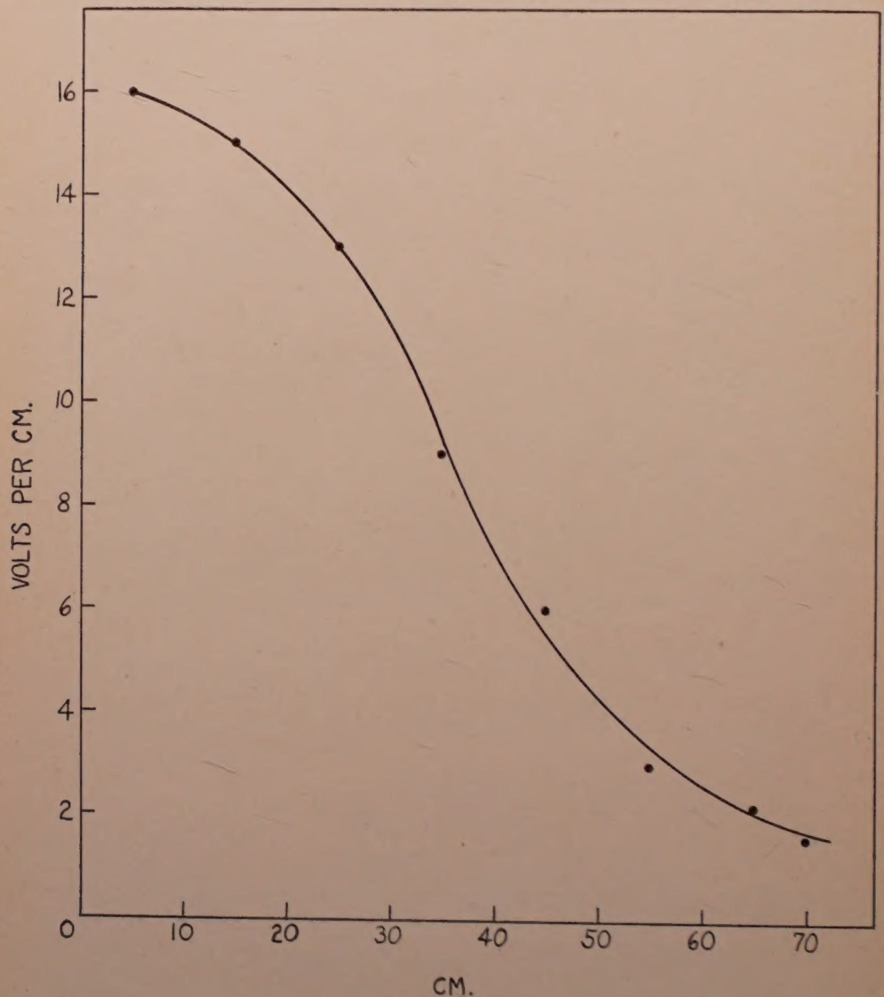
Text-fig. 1.

Major discharge. Electrodes at 10 cm. and 20 cm. from anterior end of anal fin. Reciprocal peak voltage vs. reciprocal external resistance.

It is hard to estimate the accuracy of these results. As regards the leakage resistance r, it is not so much the accuracy of the measurement itself which is in question as the accuracy of the assumption that all the current caused to flow in the adjacent tissue by the discharge of a segment of the organ can be treated as following a single path. As was pointed out in the paper already referred to[3] and as must indeed be rather obvious, this can be only a crude approximation. The error in this assumption will impair the accuracy of the determination of the internal resistance R, which is subject also to the errors of the extrapolation in the graphical method illustrated in Text-fig. 1. In what follows we are principally interested in the electromotive force E. Its values are computed from the values of the resistances and the measured values of the peak voltage by the equation

$$E = V \frac{r+R}{r} \tag{4}$$

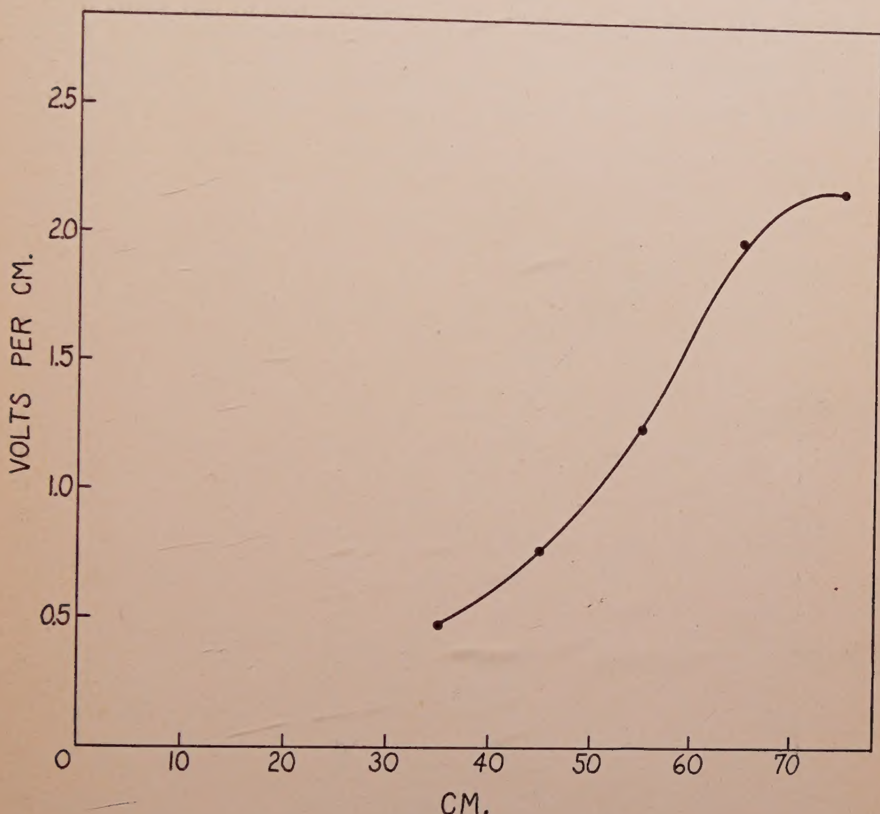
in which V is the peak voltage observed with no external conductor between the electrodes. It is seen in Table I that for about 50 cm. along the fish from



Text-fig. 2.

Major discharge. Electromotive force per cm. vs. distance along organs from anterior end of anal fin.

the anterior end of the large electric organ the measured values of r are much larger than the computed values of R in the major discharge. It seems probable that here the electromotive force actually is, as it is represented by the equation, not much greater than the peak voltage observed with no external conductor. In this case the ambiguities involved in the values of the resistances will not be very important in the determination of the electromotive force. We think it likely that the first five values of the electromotive force in Table I are not in error by more than about 10 per cent. The other values of Table I and those of Table II we consider rather more doubtful.



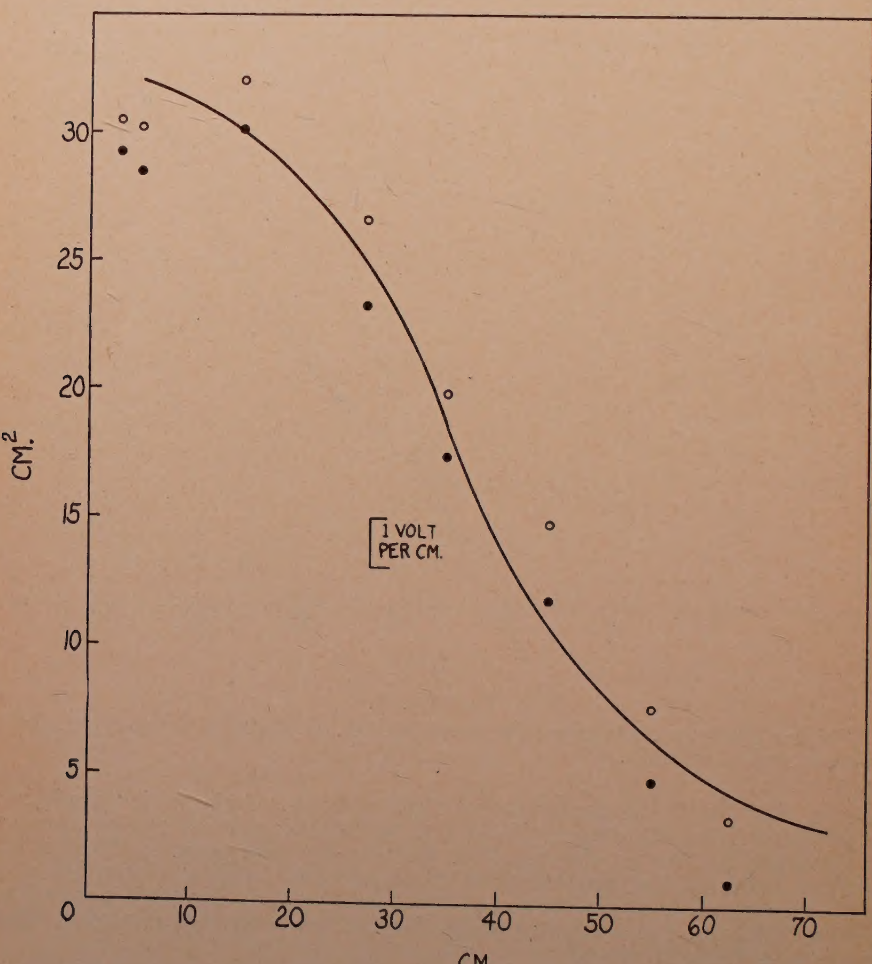
Text-fig. 3.

Minor discharge. Electromotive force per cm. vs. distance along organs from anterior end of anal fin.

In Text-fig. 2 the electromotive force per cm. of the major discharge, as reckoned from the data of Table I, is plotted as ordinate against the distance along the fish as abscissa. For plotting the first point on the left the average value of the electromotive force per cm. between electrodes at 0 and 10 cm. is taken as the value at 5 cm., and similarly for the other plotted points. Text-fig. 3 is a similar graph for the minor discharge plotted from the data of Table II.

After the measurements of the voltage and resistance were made, the fish was killed and its body transsected at a number of places. At these places the areas of the cross sections of the electric organs were measured. In Text-fig. 4 the black dots show the cross-sectional area of the large organ at various points along the fish, measured as in the other data from the anterior end of the anal fin. The white dots in the same figure show the sum

of the cross-sectional areas of the large organ and the organ of Hunter. For comparison the curve from Text-fig. 2, showing the electromotive force per cm. of the major discharge at points along the organ, has also been drawn in the figure, to the scale of volts per cm. indicated by the bracket. The fall of the plotted points along the curve is very striking. It is plain that there is a rather close proportionality between the electromotive force per cm. of the major discharge and the cross-sectional area either of the large organ alone or of the large organ and Hunter's organ together. Because of the small cross-section of Hunter's organ the ratio of area to electromotive force per cm. is not much different whether Hunter's organ be included or left out. In either case, for each 0.5 sq. cm. of cross-sectional area at any point there is found at the same point an electromotive force of approximately 1 volt per cm. along the axis of the organs. By varying the scale, either set of points can be brought closer to the curve than the other set. The best fit of the points which show the cross-section of both organs seems to be a little closer

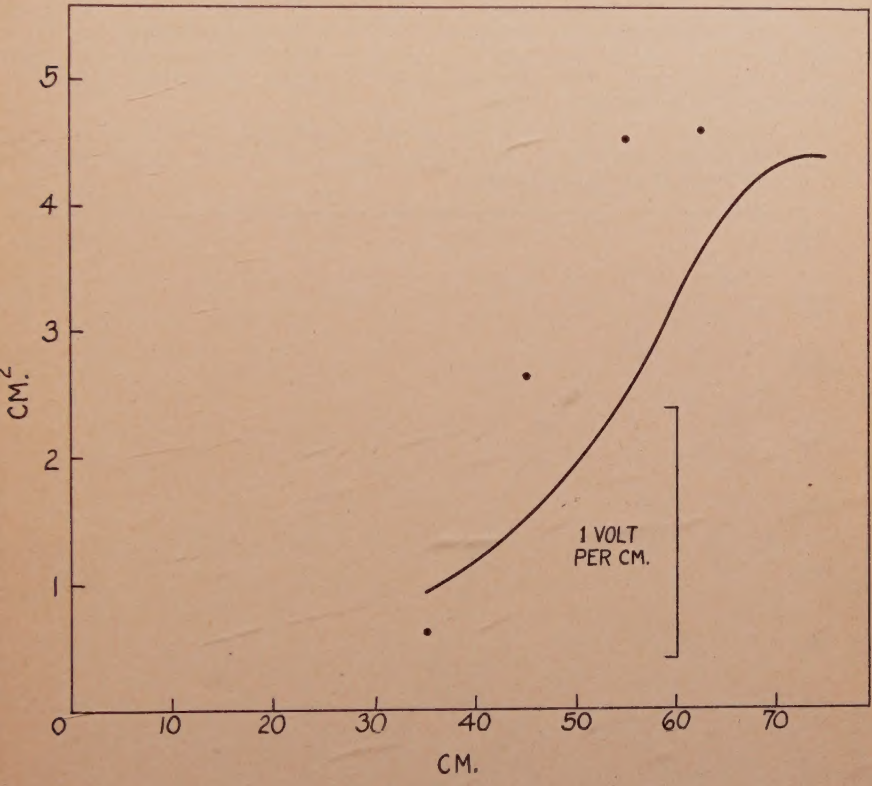


Text-fig. 4.

Curve: major discharge, electromotive force per cm. vs. distance along organs. Black dots: Large organ, cross-sectional area vs. distance along organs. White dots: Large organ and Hunter's organ, cross-sectional area vs. distance along organs.

than the best fit of the points showing the cross-section of the large organ alone, but there is not much to choose between the two.

The significance of this proportionality between the electromotive force per cm. and the cross-sectional area is not yet clear. If, in the discharge, the current were the same through every cross-section of the organ, then the observed relation would mean that equal quantities of power were generated in equal volumes of the electric tissue, since power is the product of electromotive force and current. But the current can scarcely be continuous along the organ when the fish discharges under water, since the whole skin is conducting.



Text-fig. 5.

Curve: minor discharge, electromotive force per cm. vs. distance along organs. Dots: Sachs' organ, cross-sectional area vs. distance along organs.

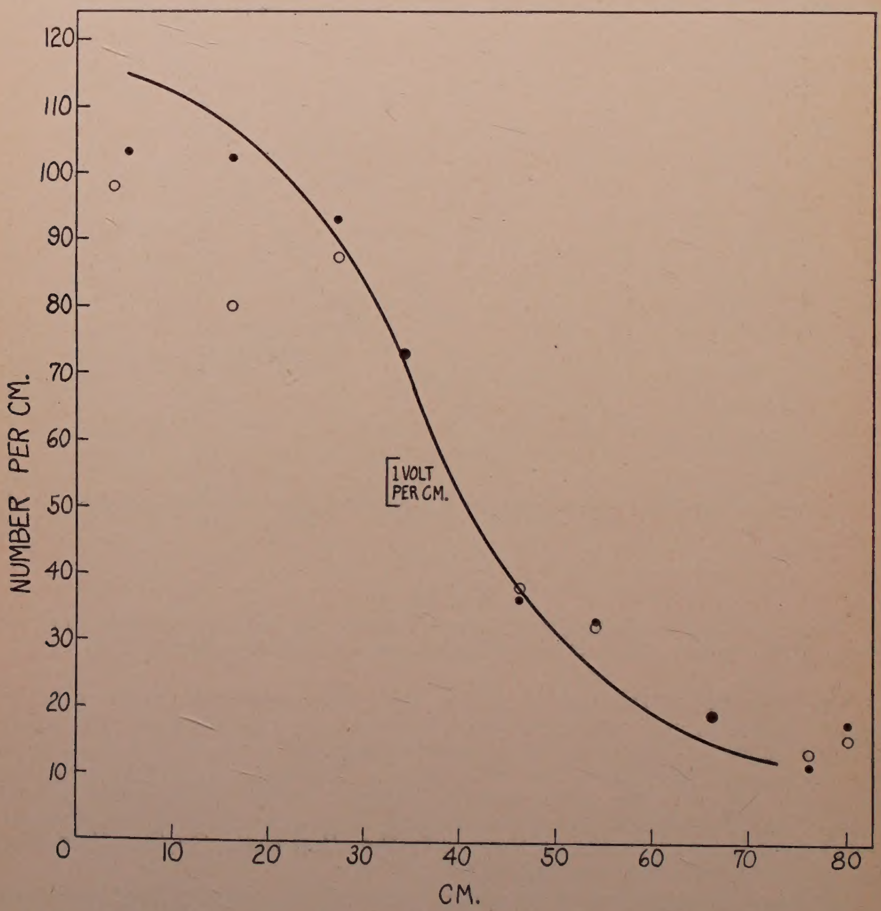
In Text-fig. 5, the plotted points show the cross-sectional area of the organs of Sachs and the curve shows the electromotive force per cm. of the minor discharge. The scales of area and electromotive force per cm. are not the same as in Text-fig. 4, but their ratio is the same. By choosing another value for this ratio, the points could be brought nearer to the curve, but the proportionality between the electromotive force per cm. and the cross-sectional area is by no means as clear as in the other case. On the other hand, the measurements are less dependable.

Transverse segments of the body of the fish were also divided sagittally, and the exposed surface of electric tissue was stained with methylene blue. The number of electroplaxes per cm. in the direction of the length of the fish, which is also the direction of the electric polarity, was counted under the microscope in each of the organs at various points along them. The septa of the electric tissue are tough but the matter they inclose is watery and

the tissue is therefore easily misshapen after being cut. This distortion of the cut surface could not be entirely prevented but was limited by mechanical means. The probable error of the count is estimated at less than 10 per cent along the greater part of the large organ and Hunter's organ, and somewhat more elsewhere.

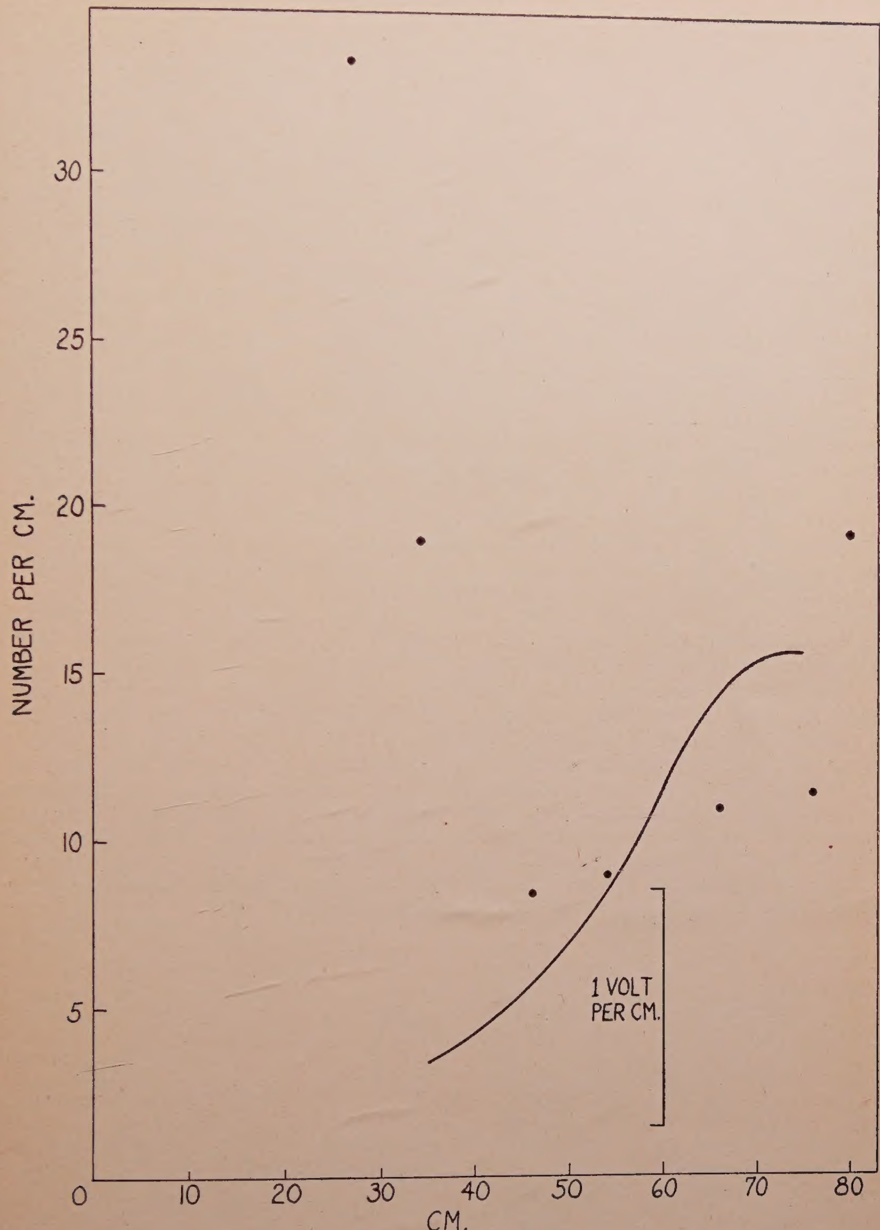
In Text-fig. 6, the black dots show the number of electroplaxes per cm. at various points along the large organ, and the white dots show the number per cm. along the organ of Hunter. Except at one place there is no difference between them too great to be a probable error of measurement. The curve showing the electromotive force per cm. of the major discharge is also drawn here for comparison. Again the plotted points fall rather close to the curve, and here the proportionality between the two plotted quantities has a clear enough meaning, which is simply that the electromotive force of one electroplax is at least roughly the same all along the organ. From the data plotted in Text-fig. 6 it is about 0.14 volt.

Dr. Kenneth S. Cole, using the needle technique, has found a change in potential during activity in the squid axon of 0.16 volt, and in *Nitella* of 0.1 volt. (Personal communication).



Text-fig. 6.

Curve: major discharge, electromotive force per cm. vs. distance along organs. Black dots: Large organ, number of electroplaxes per cm. vs. distance along organs. White dots: Hunter's organ, number of electroplaxes per cm. vs. distance along organs.



Text-fig. 7.

Curve: minor discharge, electromotive force per cm. vs. distance along organ. Dots: Sachs' organ, number of electroplaxes per cm. vs. distance along organs.

In the first of the papers referred to above[2], the opinion was tentatively offered that Hunter's organ produced the irregular discharge to which the name intermediate was given, the major and minor discharges being more positively ascribed to the large organ and Sachs' organ. But it was observed afterward and mentioned in the second paper[3] that the power of the intermediate discharge seemed too great to be generated in Hunter's organ alone.

It was concluded therefore that Hunter's organ produced no separate discharge though it might possibly produce an irregularity in the discharge of the large organ. The similarity in the structure of adjacent parts of Hunter's organ and the large organ now leads us to question whether the large organ ever discharges alone, without Hunter's organ, or whether, on the contrary, Hunter's organ is functionally a part of the large organ, only separated from it by connective tissue and the remnant of the lateralis imus.

In contrast to Hunter's organ, which is clearly separated from the large organ but closely similar to it in structure, the organ of Sachs is hardly separated at all from the large organ but over much of its length is clearly different in the size of the electroplaxes. At the two ends of Sachs' organ, however, the electroplaxes are about as many to the centimeter as in the adjacent parts of the large organ, and appear, at least with the crude staining and under the low magnification employed in these observations, to be practically identical with them. Especially toward the posterior end the organs become indistinguishable, the septum between them being no more marked than the septa within each organ. Toward the anterior end the two organs remain distinguishable by the sizes of the electroplaxes, at least until a place is reached at which the cross-section of Sachs' organ is very small indeed, containing only a few electroplaxes in parallel.

As shown by the points in Text-fig. 7, the number of electroplaxes per cm. in Sachs' organ has by far its highest value at the anterior end, where the electromotive force per cm. is low, according to the measurements previously described. This is a surprising finding, as it would imply that the single electroplax of Sachs' organ in this part has a much lower electromotive force than the neighboring and similar electroplax of the large organ. This seems so unlikely as to require further evidence before it can be accepted.

Preliminary measurements leading to the work here described were made in 1937 at the Museu Goeldi of Pará, Brazil, by the New York Aquarium-New York University Expedition to study the electric eel. It is a pleasure to acknowledge again the generous grant to this expedition made by the Doctor Simon Baruch Foundation and to express again our thanks to Dr. Godofredo Hagmann of the Museu Goeldi and to many others who aided the research at that time. The present data were obtained at the Biological Laboratory of the Long Island Biological Association at Cold Spring Harbor. We are very grateful to Dr. Eric Ponder and others at the Laboratory for the help and encouragement we received from them.